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Past, present, and future distribution of Afromontane rodents (Muridae: *Otomys*) reflect climate-change predicted biome changes

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Abstract: Climate change constitutes a potential threat to montane biodiversity, particularly in low-altitude, tropical mountains; however, few data exist for the Afromontane taxa. In South Africa, the temperate grassland and fynbos biomes are mostly associated with the Great Escarpment and the high-lying central plateau. Varying contractions of the grassland and fynbos biomes are predicted under different climate scenarios by 2050. Animal taxa adapted to these biomes should suffer similar range declines and can be used to independently test the vegetation models. We constructed MaxEnt models from 271 unique locality records for three species of montane and submontane vlei rats that are closely associated with grassland (*Otomys auratus*, Wroughton 1906), mesic savanna (*Otomys angoniensis*, Wroughton 1906), and fynbos (*Otomys irroratus*, Brants 1827) biomes in South Africa. Projected range shifts under the A2 emission scenario of the Intergovernmental Panel on Climate Change showed increases (*O. angoniensis*) and decreases (*O. auratus*) that closely mirrored those expected for the savanna and grassland biomes, respectively. Comparison of historical (from 90 years ago) and current occurrence data from a zone of sympatry in the tropical Soutpansberg Mountains (at 1250 m asl) showed complete replacement of the grassland-adapted rodent species (*O. auratus*) by the savanna-adapted species (*O. angoniensis)* due to historically documented changes from a grassland-dominated to thicket-dominated landscape.

Keywords: ecological niche models; grassland, savanna; South Africa; vlei rats.

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Introduction

Using ecological niche models (ENMs), the boundaries of different vegetation biomes in South Africa have been predicted to vary with future climate change, with the magnitude of such changes depending on the severity of different climate change scenarios (Driver et al. 2012). In particular, the temperate grassland biome niche is expected to contract considerably by 2050 (particularly under medium-risk and high-risk scenarios) with a concomitant increase in the subtropical savanna biome. Similar results have been predicted using plant growth models to simulate a 2°C increase in temperature and 15% decrease in rainfall (Ellery et al. 1991). Plausibly, these hypothetical biome shifts could be tested by constructing ENMs for related groups of plant or animal species having distributions closely tied to either grassland or savanna biomes. Should projected range declines in temperate grassland-associated species of plants and animals be shown to be as marked as predicted by the vegetation niche models, this could have important conservation consequences for the species and communities concerned.

The speciose rodent genus *Otomys* contains some 31 species of herbivorous, mesic grassland-habitat "vlei rats" distributed widely mostly throughout Afromontane regions of southern, eastern, central, and western Africa (Taylor 2013, Monadjem et al. 2015). Recent research has shown that many of these taxa are range restricted, occurring in just one or a few adjacent mountain ranges (Taylor et al. 2009a,b, 2011, 2014, Engelbrecht et al. 2011). In southern Africa, recent studies showed that the widespread vlei rat (*Otomys irroratus sensu lato*) comprises two distinct genetic species, *O. irroratus sensu stricto* and *O. auratus*, whose distributions correspond

remarkably closely with the boundaries of the fynbos and grassland biomes, respectively (Figure 1; Taylor et al. 2009b, Engelbrecht et al. 2011). In this study, *O. irroratus* hereafter refers to *O. irroratus sensu stricto*. In the Eastern Cape, *O. irroratus* occurs also in the Albany Thicket biome and even marginally into the savanna and Nama Karoo biomes (e.g. in the Fish River valley) (Taylor et al. 2009b, Engelbrecht et al. 2011). A third southern African species (*O. angoniensis*) is distinguishable from *O. auratus* and *O. irroratus* based on craniodental characters but has been shown to occur in mesic savanna habitats on the lower slopes and proximity of mountains or escarpments, where it has a mostly allopatric distribution relative to *O. auratus* except at narrow contact zones usually located at the interface of the grassland and savanna biomes, around 1000 m in KwaZulu-Natal and Swaziland (Figure 1; Monadjem 1998, Taylor 1998) and 1300 m in Limpopo Province (Nengovhela 2014). Where *O. auratus* and *O. angoniensis* co-occur at the same site, *O. auratus* is associated with sedges and grasses adapted to densely vegetated wetlands with wet soils, while *O. angoniensis* is associated with plant species that typically grow in the drier margins of wetlands (Davis 1973).

The overall aim of this study was to model the current and projected future (2050) distributions of the three biome-associated taxa of *Otomys* mentioned above in

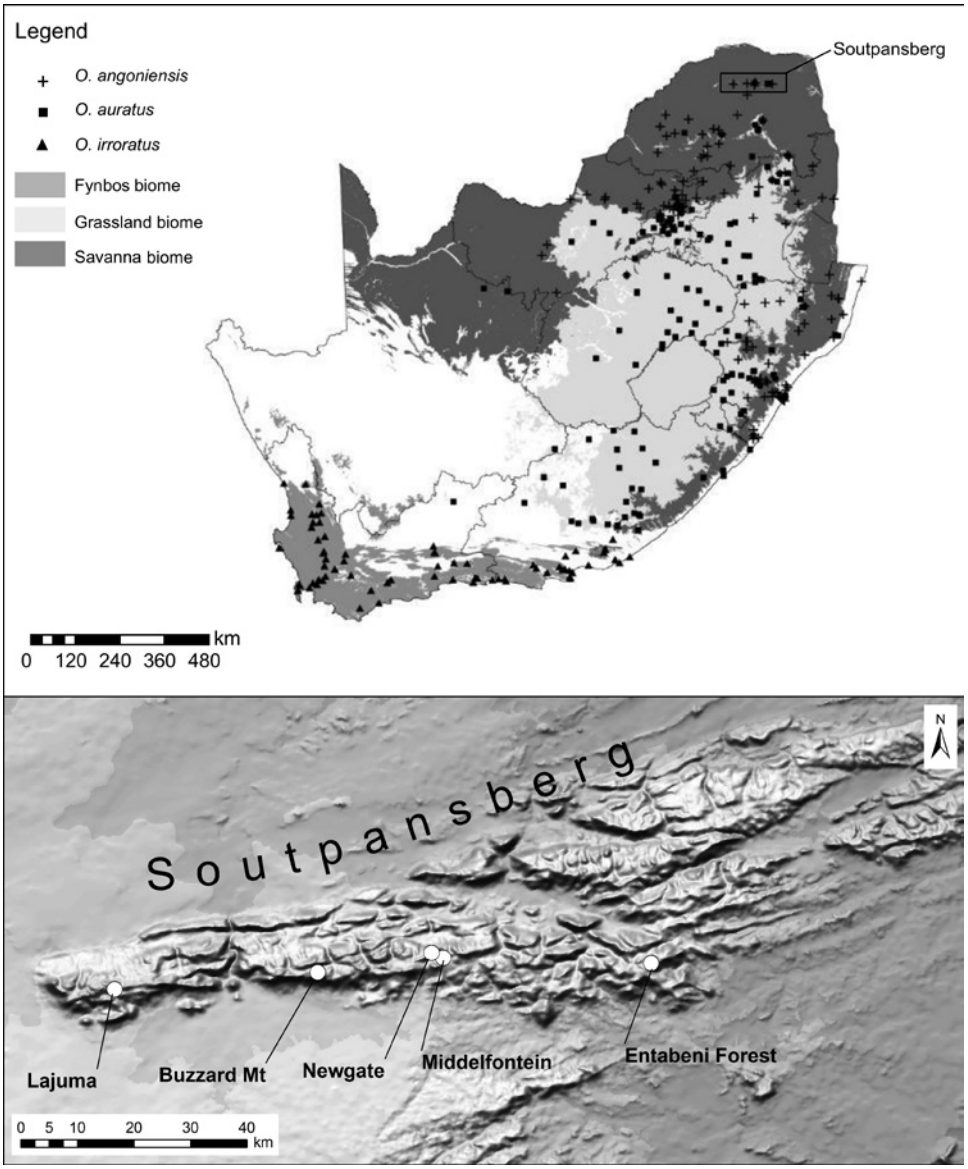

Figure 1: Map showing the distribution of three *Otomys* species in South Africa and the distributions of three major vegetation biomes (Mucina and Rutherford 2006) associated with them as well as a more detailed map of collecting localities in the Soutpansberg Mountains where we compared historical and recent collections (see text for details).

relation to the previously projected changes in the limits of their respective biomes. ENMs have been used to predict suitable habitats of rare species for their conservation management (e.g. Armstrong 2009, Tarrant and Armstrong 2013) as well as to predict niche shifts of species due to future climate change (Erasmus et al. 2002, Coetzee et al. 2009, Monadjem et al. 2012, García-Domínguez et al. 2014). Climate change is expected to cause significant biodiversity losses in the future, including in South Africa (Erasmus et al. 2002, Thomas et al. 2004, Hannah et al. 2005, Pereira et al. 2010, McCain and Colwell 2011).

Recent studies have identified many biases inherent in ENMs, including the inability of available environmental layers to estimate the fundamental niche, inappropriate backgrounds (leading to either overfitting or truncated responses), and the failure to account for dispersal capabilities as well as anthropogenic habitat transformation. These biases are particularly important where models are used to project habitat suitability to future climate scenarios. In this study, we have followed recent studies in attempting to correct for biases due to background extent (van der Wal et al. 2009, Anderson and Raza 2010), dispersal capability (Midgley et al. 2006), and habitat transformation (using the national land cover database presented in Driver et al. 2012). By doing so, we aim to test the robustness of the developed models.

Historical changes can provide clarity and confidence about the nature of ongoing and predicted future changes. For example, historical vegetation changes due to shrub encroachment in Swaziland elucidated by remote sensing of aerial photography were confirmed by recorded changes in bird communities (Sirami and Monadjem 2012). Bush encroachment is an ongoing problem that is expected to be exacerbated in the future by elevated CO_2 levels associated with climate change (Bond et al. 2003, Kgope et al. 2010) as well as by land management factors (Roques et al. 2001, Bond 2008, O'Connor et al. 2014). In order to attempt to ground-truth our models about future climate change in two of the three modeled species of *Otomys*, and to investigate the possible role of vegetation changes such as bush encroachment, we sampled *Otomys* at two historical contact zones between *Otomys angoniensis* (a mesic subtropical savanna species) and *O. auratus* (a temperate grassland species) in the Soutpansberg Mountains (Limpopo Province) and Rietvlei Nature Reserve (Gauteng Province) to compare current species composition with that recorded by historical collections from the same sites 90 and 40 years ago, respectively. To correlate these community changes with vegetation changes, we compared historical and recent aerial and satellite photographs of these sites.

Materials and methods

Occurrence data

Museum specimen records from the Ditsong National Museum of Natural History (TM) and the Durban Natural Science Museum (DNSM) supplemented with field collecting (34 nights of standard small-mammal live-trapping and *ad hoc* collection of owl pellets containing *Otomys*) in the Soutpansberg and Waterberg mountains of Limpopo Province and the Rietvlei Nature Reserve of Gauteng Province (Table 1), resulted in 271 unique South African locality records of three *Otomys* species, *O. angoniensis*, *O. auratus*, and *O. irroratus sensu stricto*, that were used for model creation (Figure 1). Species identification of museum and field-collected specimens was checked by PJT (DNSM) and AN (TM) using existing keys (Meester et al. 1986, Taylor 2013, Monadjem et al. 2015), and those that could not be correctly identified were excluded from model building. Accurate identification of *O. auratus* and *O. irroratus* from *O. angoniensis* depends on detailed inspection of cranial and dental characters. *Otomys auratus* and *O. irroratus* both have a round petrotympanic foramen and six laminae in the third lamina of the upper third molar, while in *O. angoniensis*, the petrotympanic foramen is slit-like in shape and there are seven laminae of the third upper molar (Meester et al. 1986, Taylor 2013).

Standard small mammal live-trapping (with Sherman traps) and specimen preparation procedures were used to collect *Otomys* during this study (34 trapping nights) under collecting permits from the Limpopo Department of Environmental Affairs and Tourism (permit no. 001-CPM403-00010), and for Rietvlei Nature Reserve, with the permission of the Tshwane Municipality and Gauteng Department of Agriculture and Rural Development. Capture and handling followed the guidelines prescribed by the American Society of Mammalogists (Sikes, Gannon, and the Animal Care and Use Committee 2011).

For analysis of temporal changes in species composition of *Otomys auratus* and *O. angoniensis*, we selected two sites that were both (i) historical zones of sympatry where both species had been previously collected together (in grassland habitats near the current boundary of the grassland/savanna biomes), and (ii) which could be resampled during the course of the current study. The sites included the adjacent farms of Newgate and Middelfontein in the central Soutpansberg Mountains in Limpopo Province and the Rietvlei Nature Reserve near Pretoria in Gauteng Province. On the basis of an unpublished personal diary of Austin Roberts in the archives of

Table 1: Localities sampled for vlei rats (*Otomys angoniensis* and *O. auratus*) in northern South Africa during this study, and from two historical collections, with the total number of nights of trapping and specimens captured or recorded from owl pellets.

Locality sampled, including farm name and number	Dates	Longitude	Latitude	No. of nights trapping (& "trap-nights")	Total no. recorded	*O. angoniensis*	*O. auratus*
Live trapping, this study (2010–2013)							
Lajuma Research Center [Farm Bergplaats (Vluchtkraal) 40 LS]	23–28 Jun 2010; 13–17 Sep 2010; 22–25 Oct 2010	29.429	-23.025	12 (600)	8	8	0
Buzzard Mountain Resort (Farm Rudyard 244 LS)	16–19 Jun 2011	29.752	-22.998	3 (150)	4	4	0
Rietvlei Nature Reserve, Gauteng Province	29 Oct–1 Nov 2012; 24 Apr–8 Jun 2013	28.280	-25.873	45 (?)	23	3	20
Portion 4 of Farm Middelfontein 803 MS, Soutpansberg Mountains	26–29 Oct 2011; 10–13 May 2012; 09–12 Aug 2013	29.9515	-22.975	9 (1350)	4	4	0
Entabeni Forest Plantation	27–31 May 2013, 4–7 Oct 2013	30.282	-22.983	7 (910)	2	0	2
Owl pellet collections, this study (2011)							
Makapansgat	8–9 Jun 2011	29.1967	-24.140	NA	1	0	1
Entabeni Game Reserve	8–9 Jun 2011	28.8569	-24.414	NA	69	69	0
Historical trapping (Ditsong National Museum of Natural History, Pretoria and Davis, 1973)							
Farm Newgate 202 MS, Soutpansberg Mountains	8–25 Jul 1923 (A. Roberts)	29.933	-22.967	17 (?)	8	2	6
Rietvlei Nature Reserve, Gauteng Province	Mar 1970–May 1972 (R.M. Davis)	28.283	-25.883	56 (5600)	375	42	333

Historical records were obtained from the Ditsong Museum mammal collection and Davis (1973). The number of traps set per night was often unknown, preventing the calculation of the number of "trap-nights" (number of collecting night multiplied by the number set per night). Where it is available, it is added in parentheses below.

the Ditsong Museum, Newgate Farm in the central Soutpansberg (altitude 1280 m asl) was sampled by Austin Roberts between 8 and 25 July 1923 (17 trapping nights), and resampled by us (at the adjacent Middelfontein Farm with similar habitat; altitude 1240 m asl) over nine trapping nights between October 2011 and August 2013. A "trapping night" is here defined as the number of nights of trapping irrespective of the number of traps set per night, which was unknown in most cases. The second site (Rietvlei Nature Reserve) was part of an intensive PhD study by R.M. Davis that resulted in 375 *Otomys* captured over 56 nights of trapping between March 1970 and May 1972 (Davis 1973); it was resampled from 29 October to 1 November 2012, but with no *Otomys* collected, where after we were able to obtain 23 *Otomys* of both species collected as part of the ongoing MSc thesis of Gerhard Goldner based at University of Pretoria (Table 1).

ENMs of current and future distribution

The field and museum data sets of *Otomys auratus*, *O. irroratus*, and *O. angoniensis* were modeled using MaxEnt (Maximum Entropy version 3.3.3 k) (Phillips et al. 2006, Elith and Leathwick 2009). MaxEnt has been shown to outperform alternative ENM software programs such as GARP and BIOCLIM (Elith et al. 2006). ArcMap version 10.1 (www.esri.com) was used to manage the occurrence records and to project (to GCS-WGS-1984) and prepare the predictor variable dataset (interpolated climatic variables) including their background. Locality coordinates were extracted directly from museum specimen labels or from official gazetteers. Records from unknown localities were not included in the model, and the remaining records were plotted on maps and inspected visually to detect obvious errors. Duplicates (records from the same pixel) were removed.

For present and future climate scenarios, eight continuous climatic variables (BIOCLIM) were used as predictors in the MaxEnt models: Bio 01 (annual mean temperature), Bio 04 (temperature seasonality), Bio 05 (maximum temperature of the warmest month), Bio 06 (minimum temperature of the coldest month), Bio 12 (annual precipitation), Bio 13 (precipitation of the wettest month), Bio 14 (precipitation of the driest month), and Bio 15 (precipitation seasonality). These variables were extracted from the CliMond website (Kriticos et al. 2012; https://www.climond.org). As animals may respond to either mean or extreme climatic conditions in addition to seasonal changes (e.g. hibernation in small mammals induced by cold winters), we selected variables to represent both extreme and mean temperature and rainfall parameters in addition to an index of seasonality.

Future climate variables were based on the CSIRO-MK3.0 general circulation model under the A2 emission scenario. The A2 emission scenario was selected because there is strong evidence that alternative less "extreme" scenarios may no longer be relevant under current greenhouse gas emission rates (Beaumont et al. 2008). All the environmental variables were resampled to a grid resolution of 10 arc min (roughly 15×15 km). The occurrence data were split into 30% testing and 70% training. Models were run with and without clamping (restricting environmental variables to the range of values encountered during model training). The oldest natural history collection records corresponded closely with the timeframe of weather station records used to estimate the environmental variables used in MaxEnt modeling.

Study regions (backgrounds) that are defined too broadly may include large areas of unsuitable habitat that may bias model results, whereas study regions that are too limited in extent may result in "truncated responses" due to environmental values outside the study region being assigned to species (van Der Wal et al. 2009, Anderson and Raza 2010). To accommodate such potential biases, we used two different masks to create the background for model calibration: (i) the political boundaries of South Africa, Swaziland, and Lesotho combined; and (ii) minimum convex polygons surrounding the occurrence points for each species, with a 50 km buffer added. In the second instance, species models were calibrated using the appropriate species polygons, but projections were made using the complete South African/Lesotho/Swaziland coverage.

Biases may also be introduced by not considering the important factor of dispersal (Midgley et al. 2006). In our study, we analyzed model results with respect to two distinct scenarios of "no dispersal" and "full dispersal." In the case of no dispersal, pixels predicted by the models to occur in new areas (relative to the current distribution model) were not considered. In the case of full dispersal, pixels were retained as part of the future distribution even when they were not part of the current predicted range, irrespective of the number of intervening pixels. We did not construct an intermediate scenario as suggested by Midgley et al. (2006), as their intermediate scenario allowed for decadal dispersal shifts of one pixel per decade for rodent-dispersed *Protea* seeds; applying the same rate in our case between the current (1975) and future (2050) scenarios would have allowed for dispersal rates of eight pixels. Our empirical data did not identify any range shifts exceeding this; hence, notwithstanding

unidentified landscape barriers, the "full dispersal" model was probably the most realistic.

Five replicates were run for each model using the cross-validation setting. The regularization multiplier was set to 1, maximum number of background points was set to 10,000, maximum iterations was set to 500, and the convergence threshold was set to 0.00001. The area under the receiver operating characteristic curve (AUC) and jack-knife test were used to evaluate the model performance. The jack-knife test examines the importance of each environmental variable by removing one variable at a time and then each variable in isolation (Phillips et al. 2006). The logistic threshold "Equal Training Sensitivity and Specificity" was used for all the models because it gave the most realistic current distribution prediction for all the species in question. Values below the threshold indicate areas that are unsuitable for the species, whereas values above the threshold represent those that are suitable (Monadjem et al. 2012).

Results

MaxEnt results

Current and future (2050) predicted ranges, model parameters, and response curves of important environmental predictor variables for *Otomys auratus*, *O. angoniensis*, and *O. irroratus* are shown in Figures 2–7 and Tables 2 and 3. In addition, projected biome limits for 2050 under a medium-risk climate scenario (from Driver et al. 2012) are superimposed for the grassland, savanna, and fynbos biomes for the future distribution maps of *O. auratus* (Figure 3B), *O. angoniensis* (Figure 5B), and *O. irroratus* (Figure 7B), respectively. In all cases, test omission rates fell very close to their predicted values based on cumulative thresholds, indicative of good fit to the models (Figures 2A, 4A, and 6A).

Models trained using single species minimum convex polygons (with 50 km buffer) had considerably lower AUC values than those trained using greater South Africa as background (Table 2). Estimates of future predicted distribution also varied considerably between the different backgrounds in the case of *Otomys angoniensis* and *O. irroratus* where maps of suitable habitat resulting from single species polygon masks included areas of South Africa far outside the current distributions, such as the arid savannas of northwestern South Africa (*O. angoniensis*) and extensive northern parts of South Africa (*O. irroratus*) (Supplemental Figure 1 A,B). In both

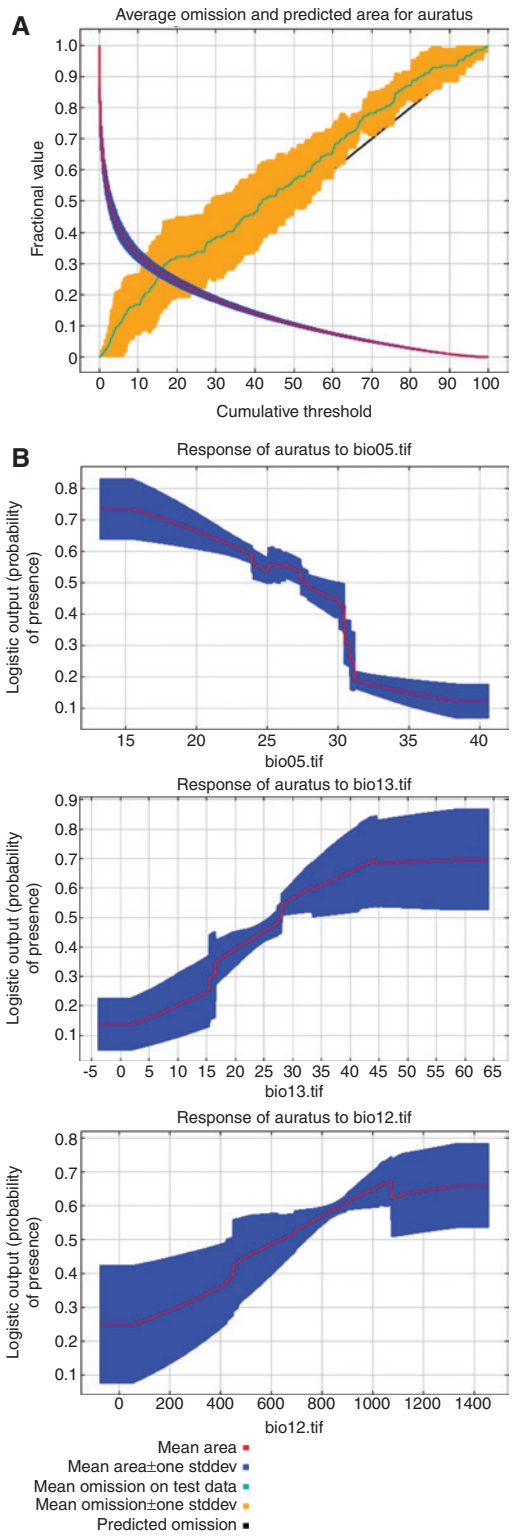

Figure 2: MaxEnt model performance and variable responses for *Otomys auratus*. (A) Test omission rate and predicted area as a function of the cumulative threshold, averaged over five replicate runs for MaxEnt model for *Otomys auratus* using the greater South African region as mask and the projection layer; (B) species response curves (means and standard deviations) for the three most important climate variables.

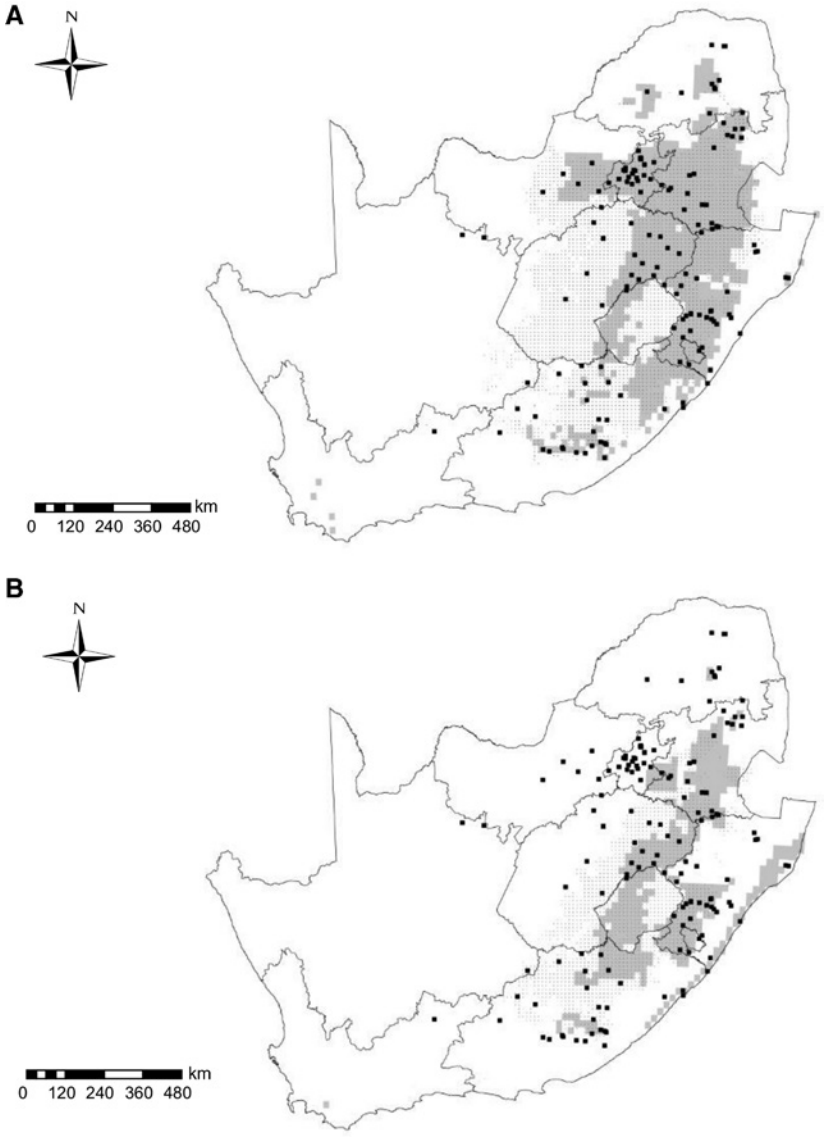

Figure 3: Maps showing MaxEnt-modeled current distribution of *Otomys auratus* (A) as well as future (B: 2050; A2 scenario) distributions of *O. auratus* based on logistic probabilities associated with the mean values obtained from five replicate models using cross-validation. The occurrence points (crosses) used for the model are included and maps are overlaid with the grassland biome limits (stippled shading), which indicate current (A) and projected 2050 (medium risk; B) limits.

these cases, clamping (restricting environmental variables to the range of values encountered during model training) resulted in different probabilities compared to models where clamping was not applied (Supplemental Figure 1 C,D), indicative of "truncated responses." Predictions in such areas affected by clamping are unreliable. Such problems encountered using minimum convex polygons for model calibration were not experienced at all using the greater South African background models, and for this reason we have based our discussion on the models trained with the South African background (Figures 2–7).

The current and future (2050) modeled distributions of *Otomys auratus* correspond broadly to the current and 2050 (medium-risk scenario) limits of the grassland biome; in both cases, distributions contract southwards (becoming extremely limited in Limpopo and Gauteng provinces) and become restricted to the higher-lying altitudes along the southeastern Great Escarpment (Figure 3). Depending on whether or not dispersal is allowed, *O. auratus* is expected to decline in area of occupancy by 47–61% by 2050 (Table 3); however, the MaxEnt model predicts an expansion of *O. auratus* by 2050 along the Indian Ocean Coastal belt, where it occurs only narrowly at present

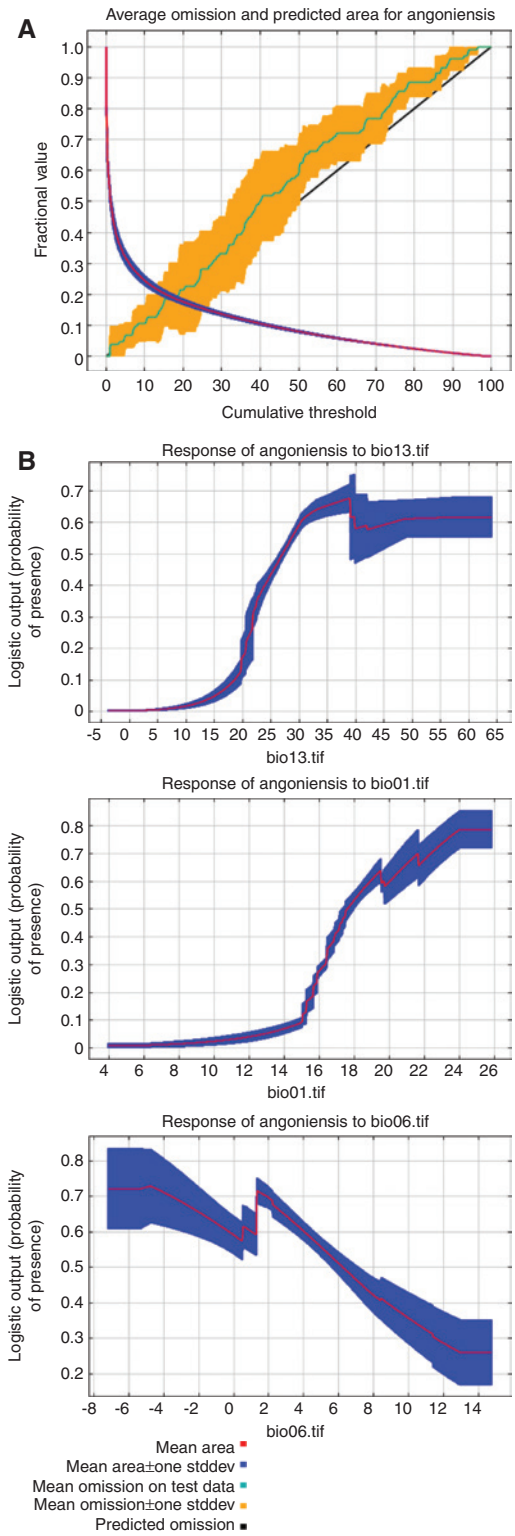

Figure 4: MaxEnt model performance and variable responses for *Otomys angoniensis*. (A) Test omission rate and predicted area as a function of the cumulative threshold, averaged over five replicate runs for MaxEnt model for *Otomys angoniensis* using the greater South African region as mask and the projection layer; (B) species response curves (means and standard deviations) for the three most important climate variables.

(Figure 3). Conversely, expected increases in the limits of the savanna biome are reflected in a predicted increase in the area of occupancy of 123% in *O. angoniensis* if unrestricted dispersal occurs; however, if dispersal is not possible, the range will decline by 30%. By 2050, the range of *O. angoniensis* is projected to extend widely into areas currently occupied by *O. auratus* in the current grassland biome (Figure 5). Future projected changes in the extent of the fynbos biome are less marked than for the grassland and savanna biomes; however, quite substantial contractions are expected for the Eastern Cape compared with the Western Cape (Figure 7). Predicted changes in the distribution of *O. irroratus* are also relatively minor (12–24% decline by 2050), with most of the declines occurring in the Western Cape. However, in the Eastern Cape, where the extent of the fynbos biome is expected to be highly reduced by 2050, the future distribution of *O. irroratus* appears little changed or even slightly larger (Figure 7), indicating that the species is not closely tied to the fynbos biome in its Eastern Cape distribution.

Suitable habitats of *Otomys auratus* are associated with cooler maximum monthly temperatures (Bio 5) and higher average (Bio 12) and wettest monthly (Bio 13) precipitation (Figure 2B). Suitable habitats of *O. angoniensis* are associated with higher precipitation of the wettest month (Bio 13), warmer mean annual temperatures (Bio 1), and cooler monthly minimum temperatures (Bio 6; Figure 4B). Suitable habitats of *O. irroratus* are associated with medium to high minimum monthly precipitation of the driest month (Bio 14), high rainfall seasonality (Bio 15), and higher minimum temperatures of the coldest month (Bio 6; Figure 6B).

Historical changes in species composition and vegetative cover

Soutpansberg Mountains

Prior to this study, *Otomys* was collected only from Newgate Farm in the central Soutpansberg (in 1923) and Entabeni Forest Station in the eastern Soutpansberg (in 1976). The present study added collections from western (Lajuma Research Station and Buzzard Mountain Retreat), central (Middelfontein Farm, 2 km from Newgate Farm), and eastern (Entabeni) Soutpansberg (Figure 1, Table 1). During Austin Roberts's 1923 survey, the grassland-associated species *Otomys auratus* appeared to be dominant at Newgate Farm in the central Soutpansberg, representing 75% of all *Otomys* captures (n=8). At the nearby Middelfontein Farm 90 years later, we caught

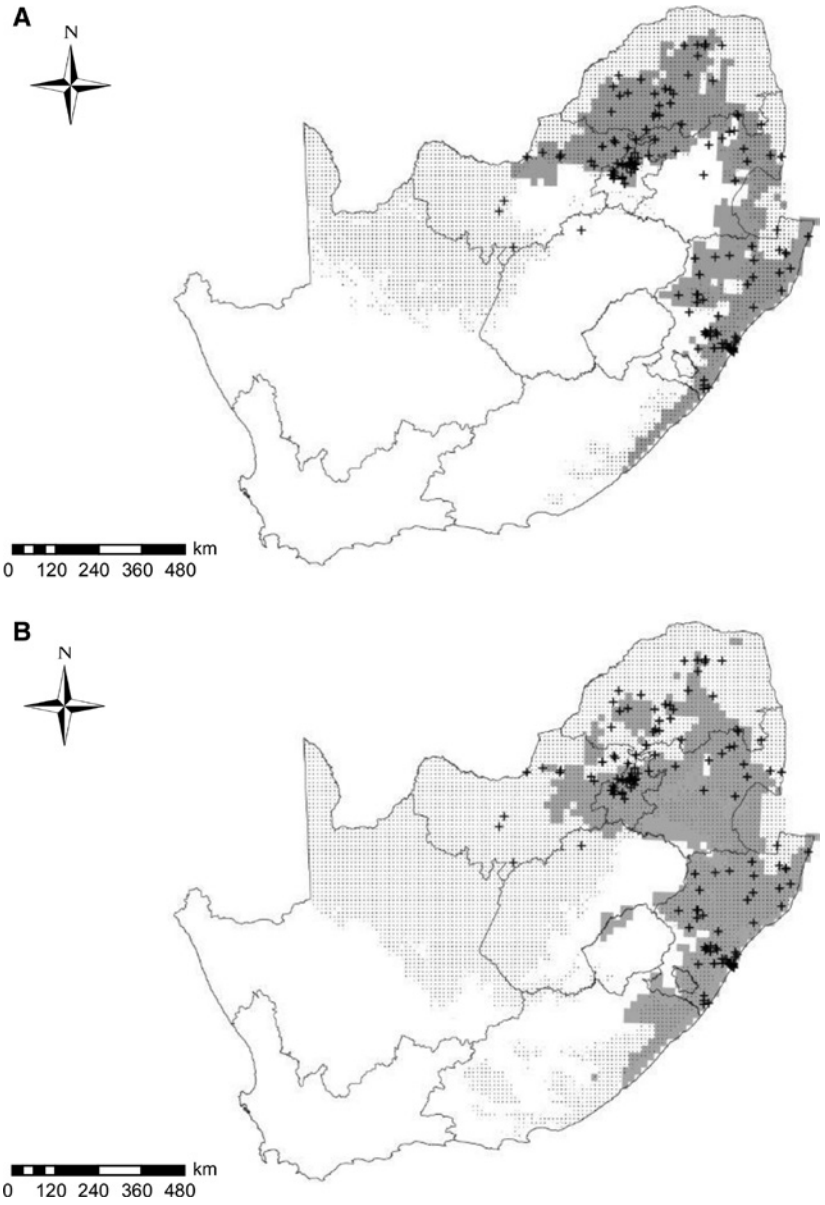

Figure 5: Maps showing MaxEnt-modeled current distribution of *Otomys angoniensis* (A) as well as future (B: 2050; A2 scenario) distributions of *O. angoniensis* based on logistic probabilities associated with the mean values obtained from five replicate models using cross-validation. The occurrence points (crosses) used for the model are included and maps are overlaid with the savanna biome limits (stippled shading), which indicate current (A) and projected 2050 (medium risk; B) limits.

four *O. angoniensis* and no *O. auratus* after nine nights of trapping with 150 traps per night (1350 trap-nights) (Table 1). Such low trap success is typical of these "trap-shy" rodents. The difference reported above in frequencies of the two species collected at adjacent sites in 1923 and 2011–2013 was statistically significant (χ^2=6.0, p=0.01). While these observations from the central Soutpansberg are localized and based on small sample sizes, data from the wider Soutpansberg support the hypothesis of regional extinction of *O. auratus*. Modern collections of *Otomys* from the western Soutpansberg (Lajuma Research Centre and Buzzard Mountain Retreat) undertaken in dense grassland habitats at high elevations >1300 m typical of *O. auratus*, revealed only the savanna-associated species, *O. angoniensis* (n=12 collected over 15 nights of trapping; Table 1). No prior collections were available for these sites. During our study, *O. auratus* was collected in the Soutpansberg only at Entabeni Forest Station in the eastern Soutpansberg (n=2, after seven trapping nights of 130 traps per night, or 910 trap-nights), where a single specimen of the same species was previously collected on 29 March 1976 (Table 1).

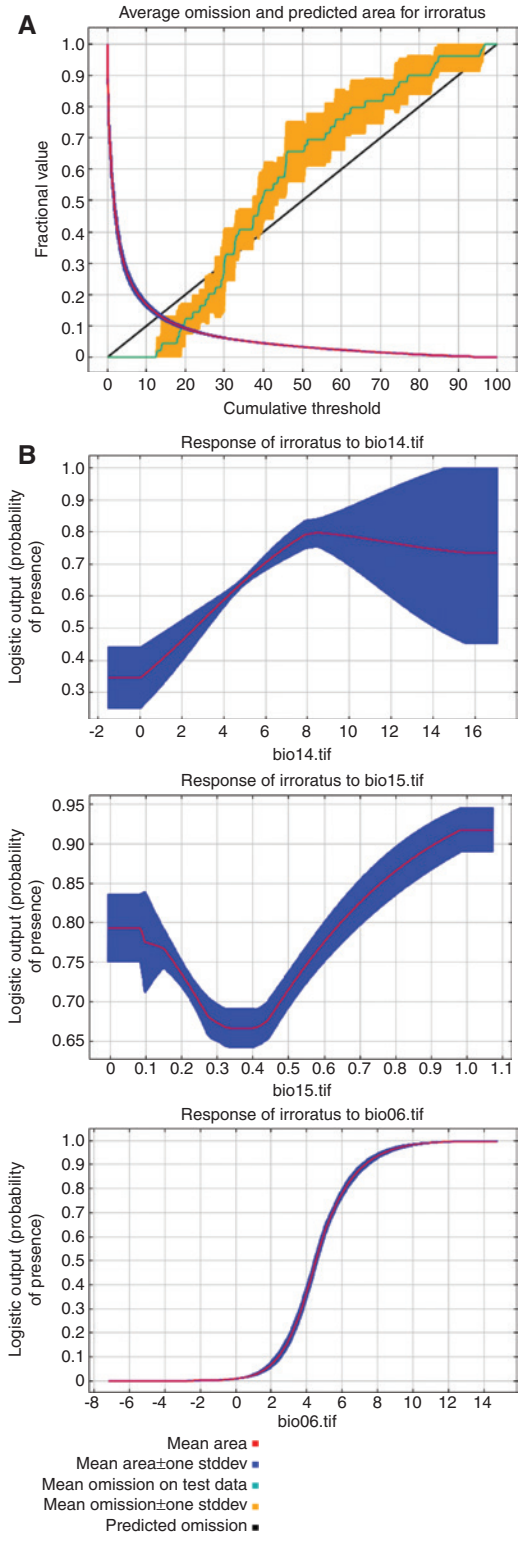

Figure 6: MaxEnt model performance and variable responses for *Otomys irroratus*. (A) Test omission rate and predicted area as a function of the cumulative threshold, averaged over five replicate runs for MaxEnt model for *Otomys irroratus* using the greater South African region as mask and the projection layer; (B) species response curves (means and standard deviations) for the three most important climate variables.

Comparisons between the aerial photographs from 1951 from the vicinity of Newgate and Middelfontein farms and modern photographs (2008) from the same area (Figure 8) reveal that the vegetation in the area has changed substantially over at least the past six decades, from predominantly open grassy plains to predominantly dense woodlands (thickets) classified currently as the Soutpansberg Mountain Bushveld (Mucina and Rutherford 2006).

Rietvlei Nature Reserve, Gauteng Province

On the same 2.25-ha grid during mostly monthly sampling from March 1970 to May 1972, Davis (1973) captured both *Otomys auratus* and *O. angoniensis* in numbers, which approximated an 8:1 ratio (333 *O. auratus*, 42 *O. angoniensis*). In Grass Owl and Barn Owl pellets collected during the same study, *O. auratus* outnumbered *O. angoniensis* by 14:1 and 9:1, respectively. A similar ratio in specimens collected was determined by the current study (20 *O. auratus*, 3 *O. angoniensis*). There was no significant difference in the frequencies reported above of the two species collected in 1970–1972 and 2013 (χ^2=0.073, p>0.05). The grassy wetland ("vlei") sites where *Otomys* was collected during 1970–1972 and again in 2013 have not changed appreciably in structure (Figure 9) between the two studies, although succession toward a climax wetland vegetation has been documented in a rehabilitation program begun in 2000 for the peat wetlands previously desiccated and mined before the Pretoria City Council acquired the property in 1929 (Venter et al. 2003).

Discussion

Robustness of models to assumptions of background mask, dispersal, and habitat transformation

The background mask chosen for model calibration had an important effect on the outcome of ENMs in the case of *Otomys angoniensis* and *O. irroratus*. Choosing species polygons as masks resulted in truncated responses as diagnosed by variable probability (habitat suitability) values when clamping was applied (Supplemental Figure 1). These models using single-species masks also predicted areas of high probability that were clearly unsuitable for the species, e.g. for *O. angoniensis*, the arid Kalahari Gemsbok National Park (Supplemental Figure 1).

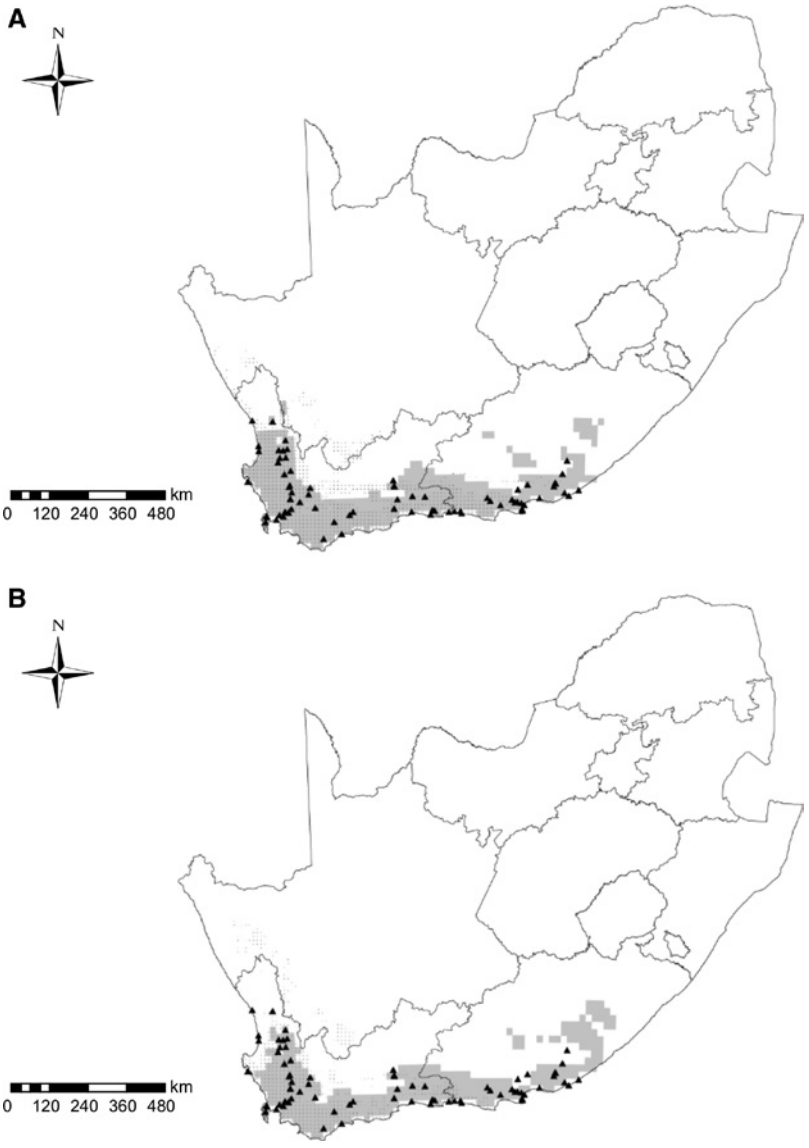

Figure 7: Maps showing MaxEnt-modeled current distribution of *Otomys irroratus* (A) as well as future (B: 2070; A2 scenario) distributions of *O. irroratus* based on logistic probabilities associated with the mean values obtained from five replicate models using cross-validation. The occurrence points (crosses) used for the model are included and maps are overlaid with the grassland biome limits (stippled shading), which indicate current (A) and projected 2050 (medium risk; B) limits.

The greater South African mask performed better than the species polygon masks (higher AUC values), was relatively free of statistical problems like overfitting, and resulted in intuitively realistic models. Using a similar approach to compare potential distributions of montane Venezuelan rodents based on a regional versus a more geographically restricted species-area mask, Anderson and Raza (2010) found that the narrower species mask performed better than the regional one. In their case, and in contrast to our study, they found that overfitting in the models calibrated with the regional-area mask resulted in unsuitable areas having apparently high probabilities, whereas the species-specific masks showed no problems of clamping and gave more intuitively realistic results. We conclude that in each study addressing these aspects, the choice of appropriate mask should be carefully considered and alternatives explored to avoid problems of both overfitting (from too broad a mask) and truncated responses (from too narrow a mask). The definition of appropriate masks based on single environmental variables such as vegetation type or rainfall is often difficult or impossible. In the case of *O. auratus*, the close association of the species distribution with the grassland biome suggests that this layer could be used to construct a suitable mask; however,

Table 2: Model parameters for five-fold cross-validation MaxEnt analyses for three species of vlei rats (*Otomys*).

Species	Mask: South Africa		Mask: single species polygons	
	AUC	Top 3 important variables	AUC	Top 3 important variables
Otomys angoniensis (n=95)	0.878±0.009	Bio13[a], Bio1[b], Bio6	0.734±0.045	Bio6[c], Bio1, Bio4
Otomys auratus (n=124)	0.822±0.036	Bio5, Bio13, Bio12[a] (Bio15[b])	0.723±0.048	Bio5[a], Bio1[b], Bio13
Otomys irroratus (n=52)	0.951±0.006	Bio14[a], Bio15, Bio6[b]	0.783±0.077	Bio12[a], Bio15[b], Bio13

No. of unique occurrences (n) given for each species. [a]Variable with highest gain when used in isolation, i.e. which has the most useful information by itself; [b]variable that decreases the gain the most when it is omitted, i.e. which has the most information that is not present in the other variables; [c]variable that satisfies both conditions [a] and [b] above.

the existence of geographically outlying records (Figure 1) could result in truncated responses when using a possibly restrictive mask. At least in this study, although it included some unsuitable (e.g. semi-arid) areas, the use of a mask corresponding to the political boundaries of South Africa, Lesotho, and Swaziland did not appear to create problems of overfitting.

Differences in dispersal scenarios affected the outcome of models, particularly in the case of *Otomys angoniensis*, where, assuming full dispersal, the 2050 predicted range will expand considerably into new areas currently occupied by *O. auratus*. Given that *Otomys* can occupy disturbed habitats such as lush overgrown lawns and gardens, young pine plantations, and rank vegetation along drainage lines and roads (Taylor 1998), they are likely to be reasonably good dispersers and the "full-dispersal" model probably applies. Indeed, our trapping data from Soutpansberg suggest that *O. angoniensis* has already replaced *O. auratus* throughout most of the mountain range except in the Entabeni area in the east.

The models presented in this study assume that suitable habitat for the species occurs in all c. 2.5×2.5 km pixels identified by the model. This is a naïve assumption as national land-cover maps (Driver et al. 2012) have demonstrated rapidly accelerating anthropogenic habitat transformation in South Africa in recent years, and this is set to accelerate even further in the near future and to have an impact on biodiversity (Chown 2010). For example, maps presented by Driver et al. (2012) for the KwaZulu-Natal Province between 1994 and 2008 reveal considerable transformation particularly in the coastal areas, with the prediction that no natural cover will persist outside of protected areas by 2050. Given that *Otomys* species may utilize some transformed habitats as indicated above, we did not attempt to subtract transformed areas from our modeled current and future areas of occupancy. Nevertheless, a "worst-case scenario" can be envisaged if we assume that no natural habitats for *Otomys* will occur outside protected areas in KwaZulu-Natal by 2050. Overlaying the map of formal protected areas over the map of the 2050 predicted distribution of *O. auratus* shown in Figure 3B, 22 out of 41 pixels of suitable habitat occurring along the coast of KwaZulu-Natal contain protected areas. If it is assumed that only protected areas will contain suitable habitat, this indicates a reduction (by about 50%) in the area of occupancy indicated by the model. Transformation of coastal areas of KwaZulu-Natal is mostly due to monocultures of sugar cane, forestry plantations, and residential developments. Depending on whether or not *O. auratus* could occupy such transformed areas, which is probably dependent on continuous areas of suitable riparian grassy vegetation around dams and along rivers, and assuming that the species will be capable of dispersing to suitable areas along the coast as the model predicts, the future distribution of the species may be highly fragmented, resulting in high rates of local population

Table 3: Area of occupancy (number of pixels) estimated for five-fold cross-validation MaxEnt models of current and future (2050) distribution for three vlei rat species with two different backgrounds (greater South Africa or minimum convex polygons based on occurrence records of each of the three species, with 50 km buffer added) and assuming either no dispersal or full dispersal.

Species	Mask: South Africa			Mask: single species polygons		
	Current	2050 dispersal	2050 no dispersal	Current	2050 dispersal	2050 no dispersal
Otomys angoniensis	658	811	467	418	585	162
Otomys auratus	776	412	306	657	255	173
Otomys irroratus	345	304	263	179	2145	124

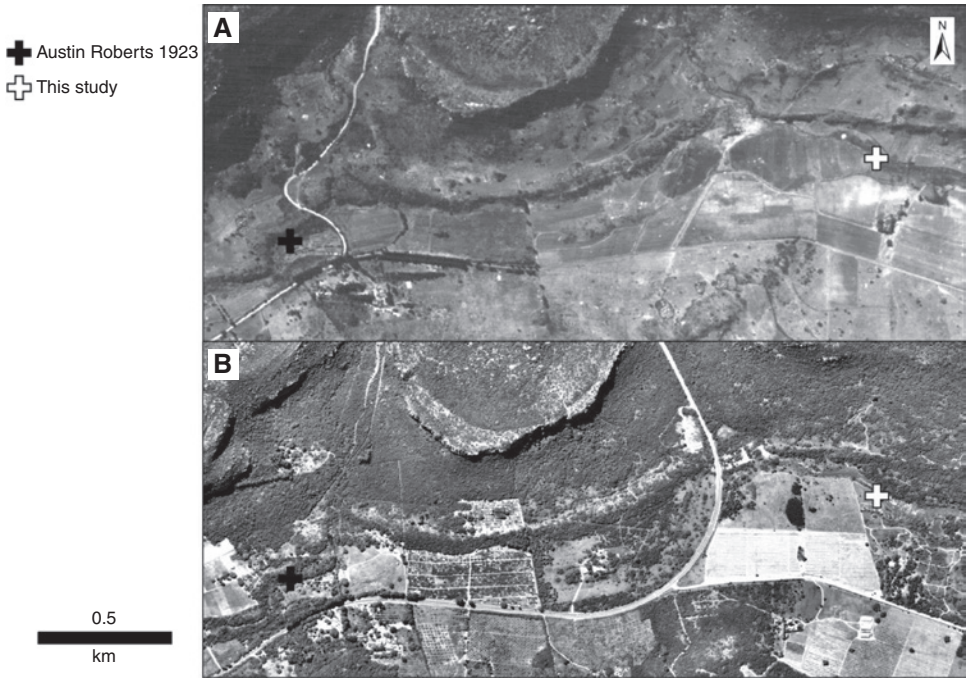

Figure 8: Aerial photographs of the central Soutpansberg in the vicinity of the Newgate and Middelfontein farms from 1951 and 2008 indicating the site of historical (1923: Austin Roberts) and current (this study) collection of *Otomys*.

extinction. Given the high rates of habitat degradation and loss across Africa, ENMs consider this factor when projecting the potential and future ranges of species.

Climate and historical change implications

General increases in mean temperatures have been documented in South Africa since the 1950s; while the extent of these increases varies spatially, the mean annual temperature in parts of northern Limpopo has been estimated to have increased by as much as 0.1°C per decade between 1950 and 1999 (Kruger and Shongwe 2004, Tshiala et al. 2011). Bioclimatic and plant growth models suggest that the climatic conditions for grasslands may be replaced in the future by conditions more favorable to savannas notably in large areas of the Limpopo, Gauteng, Northwest, and Mpumalanga provinces of South Africa (Ellery et al. 1991, Driver et al. 2012).

Our models projected changes in the distribution of *Otomys auratus* and *O. angoniensis* by 2050, which were largely congruent with the 2050 limits of grassland and (mesic) savanna biomes, respectively, projected under the medium-risk climate change scenario of Driver et al. (2012). These results confirm our prediction that under future climate change scenarios, the more tropical savanna biome species will gradually replace the more temperate grassland biome species. We also predicted a decline in the range of a fynbos biome rodent species (*O. irroratus*) consistent with expected contractions in the extent of this biome by 2050. However, while the fit between the current and future limits of *O. irroratus* and the fynbos biome was good for the Western Cape Province, there was less congruence between their respective distributions in the Eastern Cape portion of their distribution where *O. irroratus* is able to persist in the Albany Thicket biome (Taylor et al. 2009b). This seems to indicate that *O. irroratus* is a weaker indicator species for the fynbos biome than are *O. auratus* or *O. angoniensis* for the grassland and (mesic) savanna biomes, respectively.

In support of these future modeled projections for the grassland and savanna biome-associated rodent species, we also demonstrated a historical shift in dominance from *Otomys auratus* (grassland-associated) to *O. angoniensis* (savanna-associated) at one location in the Soutpansberg over a 90-year period, accompanied by extensive vegetation transition from open grassy plains to dense woodland. It is not immediately clear which components of the respective niches of the two species are responding to these observed historical changes and what environmental factors may be driving these changes. At least three hypotheses can be advanced.

1. Direct effects of increasing temperatures could confer metabolic advantages to the tropical (*Otomys angoniensis*) relative to the temperate (*O. auratus*) species. Variable responses from the MaxEnt models attest

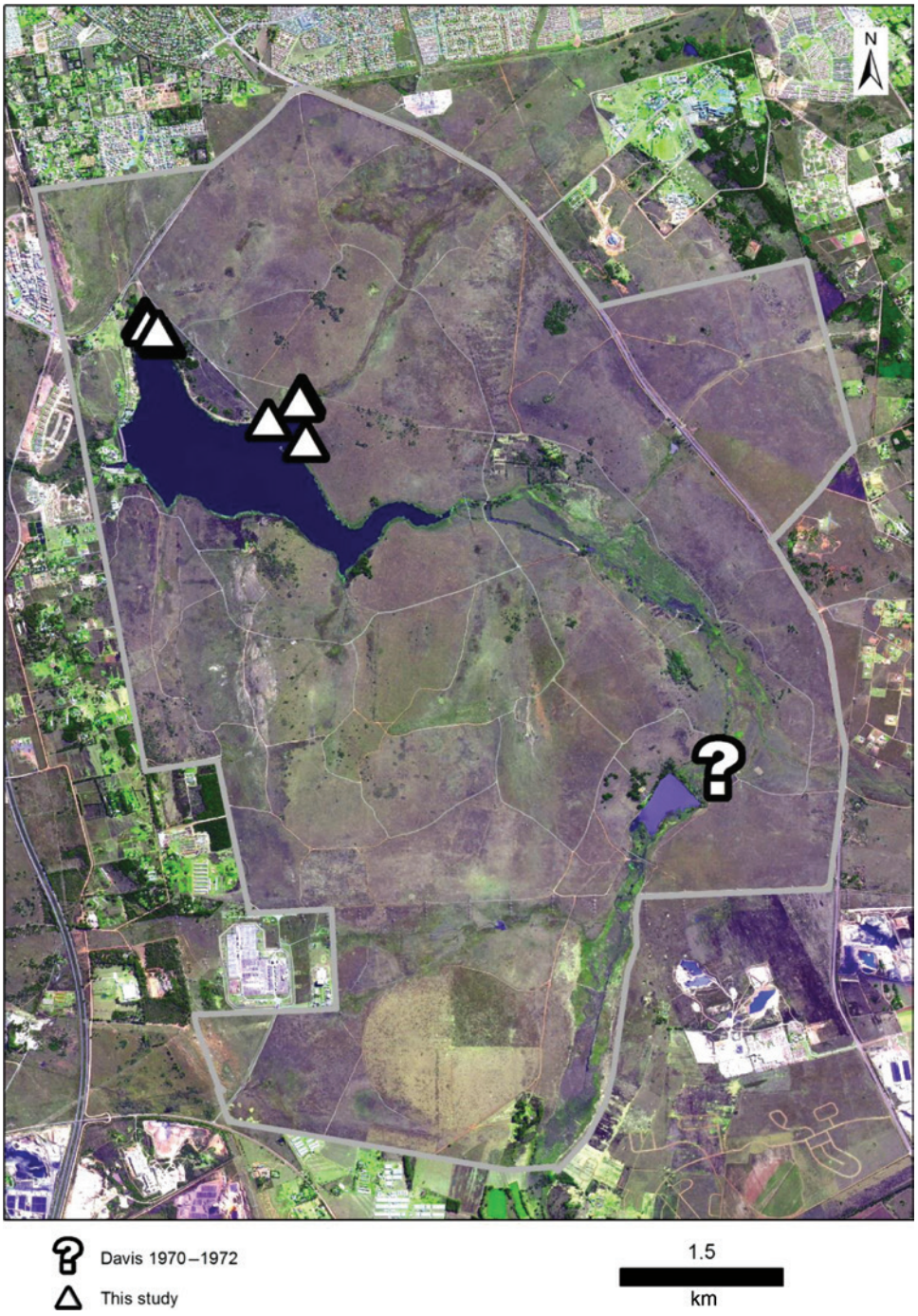

Figure 9: 2008 Satellite photograph of Rietvlei Nature Reserve (outlined) indicating the approximate area (indicated by ?) of historical (1970, 1972: Davis) collections and recent sites of collection (this study).

to the preference of *O. angoniensis* for high rainfall and warmer temperatures, while suitable habitats of *O. auratus* were associated with cooler temperatures and high rainfall (Figures 3B and 5B).

2. Higher temperatures (linked possibly with lower rainfall) could have an effect on vegetation type leading to plants adapted to drier soil moisture conditions favorable to *Otomys angoniensis*. Davis (1973) found a strong association between the microdistribution of *O. auratus* and *O. angoniensis* and different plant associations on a 2.25-ha trapping grid associated with a wetland and surrounding grasslands at Rietvlei Nature Reserve near Pretoria. Very little overlap occurred between the two species, with *O. auratus*

largely confined to the denser, waterlogged areas of the vlei and associated with sedges and other herbaceous plants known to be wetland adapted, while *O. angoniensis* occurred on the drier margins of the vlei and was associated with herbaceous plants occurring on drier soils.

3. Factors other than climate may have resulted in vegetation transitions such as bush encroachment that would have favored a tropical savanna species over a temperate grassland species. Drivers that promote bush encroachment include elevated atmospheric CO_2 levels (Bond et al. 2003, Kgope et al. 2010) particularly in mesic savannas (Bond and Midgley 2012), the absence of fire, and land management factors such as increased grazing pressure (Roques et al. 2001, Bond 2008, O'Connor et al. 2014) with implications for ecosystem function including hydrology (e.g. Huxman et al. 2005) and cascading impacts on biodiversity (Bond 2008). Consensus on the primary and secondary drivers has not been reached, and it is suggested that the process is a dynamic one with multiple drivers likely interacting and changing over time (O'Connor et al. 2014). Aerial photographs from 1951 and 2008 from the Soutpansberg study area (Figure 8) clearly attest to the effect of bush encroachment, which has transformed open grassy plains to thick woodland over much of the Soutpansberg (see also Hahn 2002, 2006, for many examples of old historical photographs depicting an earlier landscape of open grassy plains). In the area of the central Soutpansberg where we observed a historical shift from *Otomys auratus* to *O. angoniensis*, historical records document the existence of wetter conditions and substantial swamps and wetland areas in the early 20th century (including the location of the current town of Louis Trichardt), which dried up in the early 20th century, not least due to the extensive planting of exotic plantations (Hahn 2002, 2006).

Arguing against hypotheses 1 and 2, which assume a significant increase in temperature in the central Soutpansberg over the past 90 years, temperature data from 30 catchments in Limpopo Province collected over a 50-year period (1950–1999) show that changes in mean annual temperature in the Nzhelele River catchment (in which the study site falls) were only around -0.003°C to 0.005°C per decade, amounting to a maximum of around 0.05°C over the past century (Tshiala et al. 2011). However, in the adjacent Sand River catchment, changes of up to 0.1°C per decade were measured over the same period, reflecting considerable spatial variation in temperature changes measured across Limpopo Province.

Bush encroachment of savanna and grasslands has implications for biome-specific floral and faunal assemblages with avian studies, for example, showing a rapid turnover in species composition and negative effects on diversity (Hahn 2006, Sirami and Monadjem 2012). Conversely, experimental tree removal in grasslands being encroached has been shown to rapidly increase important native floral and faunal community metrics (Alford et al. 2012). Our study shows a historical shift in species composition in a bush encroached landscape further at risk from climate change, underscoring the need for historical perspective in modeling future changes.

Conservation implications

Species confined to mountains and having relatively low dispersal capabilities, such as terrestrial small mammals, reptiles, and amphibians, are expected to suffer heightened extinction risks due to the effects of climate change (McCain and Colwell 2011). This generalization is supported by the results of our study, particularly concerning the Afromontane grassland biome specialist, *Otomys auratus*. We would predict that the effects of climate change on biodiversity would be felt first and most keenly in tropical, lower-elevation mountain ranges. Our data from the Soutpansberg Range located just north of the Tropic of Capricorn confirm this prediction, where changes over the past few decades have resulted in the virtual replacement of a grassland biome species (*O. auratus*) by a savanna biome species (*O. angoniensis*). It is hardly surprising that of the 39 Sub-Saharan African rodent species that are classified by the International Union for Conservation of Nature (IUCN) as Vulnerable, Endangered, or Critically Endangered, all but two of them are species that have distributions confined to restricted montane habitats (Monadjem et al. 2015). Seven of these are species of *Otomys*, confined to equatorial and tropical mountains and mountain ranges such as the Cameroon Volcanic Line, Mt Elgon, the Eastern Arc Mountains, and Southern Highlands of Tanzania. Although the southern African species considered in this study have relatively wide ranges and are not classified as threatened, *O. auratus* and *O. irroratus* are model taxa for montane and submontane grassland and fynbos biome communities, respectively, and the projections of decreased range sizes with climate change apply equally to much rarer plant and animal members of these same montane communities where such range contractions may have more catastrophic consequences on population extinctions.

This study sounds an alarm that population declines due to climate change-induced range contractions should be considered in conservation assessments of Afromontane species of terrestrial plants and animals, particularly in the case of range-restricted species occurring on tropical and equatorial mountain ranges. In the case of Afromontane species having small or very small areas of occurrence or occupancy, and either fluctuating populations or highly fragmented habitats, projected continuing range contractions due to climate change can be used to formally justify threatened categories (Vulnerable, Endangered, or Critically Endangered) under the B1 and B2 criteria of the IUCN (2012).

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